Two-tone suppression in auditory nerve fibers of the green treefrog (*Hyla cinerea*)

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The phenomenon of two-tone suppression was studied quantitatively in the peripheral auditory system of the green treefrog (*Hyla cinerea*). Linear relationships were found between best excitatory and best suppressor frequency, between response thresholds at these frequencies, between Q_{10dB} -values of excitatory and suppressor tuning curves and best excitatory frequency, and between both Q_{10dB} -values.

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INTRODUCTION

Two-tone suppression is a property of many auditory nerve fibers in terrestrial vertebrates. The mechanism responsible for this phenomenon is still unclear, although measurements of basilar membrane movement (Rhode, 1977, 1978) and of response characteristics of VIIIth nerve fibers (e.g., Sachs and Kiang, 1968; Evans, 1975; Capranica and Moffat, 1980) and cochlear inner hair cells (Sellick and Russell, 1979) suggest that suppression results from a mechanical nonlinearity in the inner ear. In reptiles, birds, and mammals tones with frequencies both higher and lower than the best excitatory frequency of an VIIIth nerve fiber can have suppression effects. In anurans some of the fibers from the amphibian papilla and the sacculus (two of their three inner ear organs involved in sound processing) show two-tone suppression but only for suppression tones higher than the best excitatory frequency (Capranica and Moffat, 1980).

In this report we present details of the relationships between best excitatory and best suppressor frequencies, thresholds at these frequencies, and between sharpness of excitatory and suppressor tuning within the peripheral auditory system of the green treefrog (*Hyla cinerea*). These data are compared with quantitative measurements in other anurans (Liff *et al.*, 1968; Capranica and Moffat, 1980) and common functions expressing the relationships mentioned above are derived. We thus intend to broaden the basis on which models of two-tone suppression mechanisms can be tested.

I. METHODS

Green treefrogs were prepared for single unit recording from the VIIIth nerve as described in Ehret and Capranica (1980). Details of the sound generating and recording equipment are also given in that paper. Briefly, tones from two audio oscillators were attenuated relative to each other and either added and then shaped into bursts (300-ms duration, 10-ms rise and fall times, interburst interval 300 ms) or else only the excitatory tone was shaped and then added to a continuous suppressor tone. The adder output was passed through a master attenuator to control the overall sound pressure level (SPL) delivered by the earphone (closed sys-

tem). All SPLs are expressed in dB re: 20 μ Pa.

When a single unit was isolated its best excitatory frequency (BEF) and threshold at that frequency were determined by detecting a just noticeable increase in firing rate (oscilloscope, audio monitor, electronic counter). The intensity of the excitatory tone at the unit's BEF was increased to 10 dB above threshold and a second tone was added, either continuously or in bursts synchronized with the excitatory tone bursts. The frequency of the second tone was varied until we found that frequency which, with minimum intensity, produced the maximum reduction in firing rate evoked by the excitatory tone. This frequency was called the best suppression frequency (BSF). Although it is possible to totally suppress the excitatory response of many auditory nerve fibers some of the fibers with BEFs above 500 Hz could be only partially suppressed. After determining a unit's BSF and its threshold, excitatory and, when possible, suppression tuning curves were then measured.

II. RESULTS AND DISCUSSION

Our results are based on recordings from 70 auditory nerve fibers with best excitatory frequencies below 700 Hz. In comparing the identified origin of low- and mid-frequency fibers from the amphibian papilla and higher frequency fibers from the basilar papilla in the bullfrog (Feng *et al.*, 1975) it is quite certain that the fibers in our study all derive from the amphibian papilla (Capranica and Rose, 1983). Data from 14 additional fibers with BEFs below 300 Hz and excitatory thresholds above 60 dB SPL were not included because there was the possibility that they may have originated from the sacculus (Moffat and Capranica, 1976). No systematic differences in suppression effects of pulsed and continuous tones were observed and therefore the results from these two stimulus situations were combined.

All of the units with BEFs below about 500 Hz could be totally suppressed, i.e., the response to an excitatory tone at 10 dB above threshold could be reduced to the level of spontaneous activity by the addition of a second inhibitory tone. Fibers with BEFs between 500 and 600 Hz exhibited partial suppression whereas fibers with BEFs between 600 and 700

Hz were variable (9 of 13 showed partial suppression); fibers with BEFs higher than 700 Hz could not be suppressed for all intensity differences between the two tones of up to 40 dB (the highest we used). Tones producing suppression were always higher in frequency than those producing excitation.

Figure 1 shows representative excitatory and suppressor tuning curves. The low-frequency side of the suppressor tuning curve usually follows the high-frequency side of the excitatory tuning curve. The suppressor tuning curve of a fiber is generally broader than its excitatory tuning curve except when the BSF is close to the upper frequency limit (about 2000 Hz at 90 dB SPL) of the amphibian papilla. This upper limit confines the expansion of the suppressor tuning curve at high frequencies. The relationship of sharpness of excitatory and suppressor tuning can be quantified by plotting Q_{10dB} -values (BEF or BSF divided by the bandwidth of the corresponding tuning curve at 10 dB above threshold) for fibers of different BEFs as can be seen in Fig. 2(a). Q_{10dB} -values of both tuning curves increase linearly with frequency according to the equations:

$$Q_{10E} = 0.005 \text{ BEF} + 0.37, \quad r = 0.809, \quad p < 0.001, \quad (1)$$

$$Q_{10S} = 0.003 \text{ BEF} + 0.19, \quad r = 0.633, \quad p < 0.001. \quad (2)$$

The sharpness of tuning both of excitatory and suppressor tuning curves increases with BEF up to about 550 Hz and the excitatory tuning curves are always sharper than the suppressor tuning curves. This is shown more clearly in a plot of Q_{10S} vs Q_{10E} in Fig. 2(b) for a number of fibers with BEFs below 550 Hz. The data can be fitted by a linear regression line¹:

$$Q_{10S} = 0.6Q_{10E} - 0.12, \quad r = 0.833, \quad p < 0.001. \quad (3)$$

Plots of BSF vs BEF (Fig. 3) and of suppression threshold (T_S) versus excitation threshold (T_E) [Fig. 4(a)] can also be described by linear relations:

$$\text{BSF} = 1.77 \text{ BEF} + 341, \quad r = 0.876, \quad p < 0.001, \quad (4)$$

$$T_S = 0.76T_E + 34, \quad r = 0.754, \quad p < 0.001. \quad (5)$$

FIG. 1. Tuning curves of two representative fibers; excitation: open symbols, suppression: closed symbols; symbols of one shape are from the same fiber.

FIG. 2. (a) Relation between Q_{10dB} -values (Q_{10E} : open circles, Q_{10S} : closed circles) of tuning curves and the best excitatory frequency (BEF); regression lines after Eqs. (1) and (2) are also shown. (b) Q_{10S} vs Q_{10E} ; regression line after Eq. (3).

Figure 4(a) shows that for all units T_S is higher than T_E although the threshold difference can be as small as 6 dB. In Fig. 4(b) the difference between T_S and T_E is plotted against T_E and it is evident that this difference decreases with increasing excitatory threshold.

These findings from (*Hyla cinerea*) can be compared with data for BEFs and BSFs from the amphibian papilla (possibly including some sacculus units) of the bullfrog (*Rana catesbeiana*; Liff *et al.*, 1968) and of the American toad (*Bufo americanus*; Capranica and Moffat, 1980) which also follow linear functions. Bullfrog (all data shown by Liff *et al.*, 1968):

$$\text{BSF} = 1.25 \text{ BEF} + 342, \quad r = 0.81, \quad p < 0.001, \quad (6)$$

American toad²:

$$\text{BSF} = 1.64 \text{ BEF} + 324, \quad r = 0.90, \quad p < 0.001. \quad (7)$$

FIG. 3. Best suppression frequency (BSF) versus best excitatory frequency (BEF) with regression line after Eq. (4).

FIG. 4. (a) Relation between suppression threshold (T_S) and excitatory threshold (T_E) with regression line after Eq. (5) (solid line); if T_S and T_E were equal they should follow the dashed line. (b) Difference between T_S and T_E vs T_E ; the regression line can be calculated by rearranging Eq. (5).

Data on excitatory and suppressor thresholds and Q_{10dB} -values have not been published for other anuran species.

Equations (4), (6), and (7) have all similar slopes and almost the same values for BSF when BEF is zero. This agreement of BSF-BEF relationship among the three anuran species studied may be due to the similar shapes of their amphibian papillae (Lewis, 1978) and similar transition regions between low-frequency fibers which can be suppressed and mid-frequency fibers which cannot be suppressed. These transitions are near 650 Hz in *H. cinerea*, and near 550 Hz in *R. catesbeiana* and *B. americanus* (Feng *et al.*, 1975; Capranica and Moffat, 1980). The similarity of Eqs. (4), (6), and (7) thus can be taken as evidence for a common mechanism of suppression of low-frequency units in the amphibian papilla of these species.

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¹ For fibers with BEFs higher than 550 Hz the high-frequency side of the suppressor tuning curve was substantially confined by the upper limit of the amphibian papilla's frequency response. Therefore Q_{10dB} -values of these fibers are not included in the regression analysis of Eq. (3).

² Capranica and Moffat (1980) approximated these data by a power function with a correlation coefficient of $r = 0.93$. The correlation coefficient for a linear approximation (Eq. 7) of $r = 0.90$ indicates also a significant relation so that the data fit both a linear and a power function with similar statistical significance.

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